

MORPHOLOGY, ECOLOGY AND ASEYUAL
REPRODUCTION OF A NEW *POLYDORELLA* SPECIES
(POLYCHAETA: SPIONIDAE) FROM THE
SOUTH CHINA SEA

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ABSTRACT

A new polychaete species, *Polydorella dawydoffi* (Spionidae) is described from the South China Sea, Vietnam. The species attains a length of 2 mm forming 15 segments and reproduces asexually by paratomy, with the paratomic growth zone appearing between segments 11 and 12. Sexual reproduction was not observed. *Polydorella dawydoffi* constructs mud tubes on the surface of sponges occurring at 3–10 m depths. Density of colonies reaches up to 130 individuals·cm⁻² on the sponge surface. A key to the four known *Polydorella* species is provided together with a diagnosis of the genus. As all known *Polydorella* species are associated with sponge surface, a unique feature within the polydorids, it is suggested that the characteristics (apomorphies) of the genus were developed in the most common ancestor in association with this specific habitat.

Augener (1914) established the genus *Polydorella* which was characterized by having a modified fourth segment in contrast to *Polydora* and related spionid genera which have segment 5 modified. Blake and Kudenov (1978) examined two syntypes of *Polydorella prolifera* and demonstrated that the 5th segment is actually modified rather than the 4th. When discussing the status of the genus, Blake and Kudenov emphasized one of *Polydorella*'s characteristic features only—the tendency for reduction of setiger 1. They proposed that this reduction is in part explained by the mode of asexual reproduction, and placed *Polydorella* into synonymy with *Pseudopolydora*. Tzetlin and Britayev (1985), however, proposed that *P. prolifera*, *P. stolonifera* and *P. smurovi* form a coherent group of phylogenetically related species characterized by the following features: reduced number of branchiae or branchiae lacking; total reduction of notopodia of first segment; few and constant number of setigers; special structure and arrangement of setae of the 5th segment. They reestablished the genus *Polydorella* Augener for these three species and emended the diagnosis.

A new spionid species, corresponding to the Tzetlin and Britayev's diagnosis of *Polydorella*, is reported from the South China Sea, Vietnam. In the present paper, morphology, ecology and asexual reproduction of the new *Polydorella* species is described, and suggestions regarding the evolution of the genus are provided.

MATERIALS AND METHODS

Specimens were collected during two expeditions by the Institute of Marine Biology, Vladivostok, to the South China Sea: with the R/V AKADEMIK ALEXANDER NESMEYANOV in January–March 1986 from Gulf of Thailand (Siam): Phuquoc Island, Thom Island of the Anchoi Archipelago, Thochu Islands (Panjang), and from Nhatrang Bay; and with the R/V BERILL in September 1988 from Nhatrang Bay and Bengoi Bay. Localities are indicated in Figure 1. Subtidal collecting was made by the author using SCUBA equipment. Analyses of samples took place on the research vessels and at the Institute of Marine Research (formerly the Institute Océanographique), Nhatrang. Specimens were relaxed in isotonic magnesium chloride prior to examination. Descriptions are from live material, and sketches prepared with the aid of a camera lucida. Different described stages of asexual reproduction do not represent growth stages from a single specimen, but selected individuals from natural conditions.

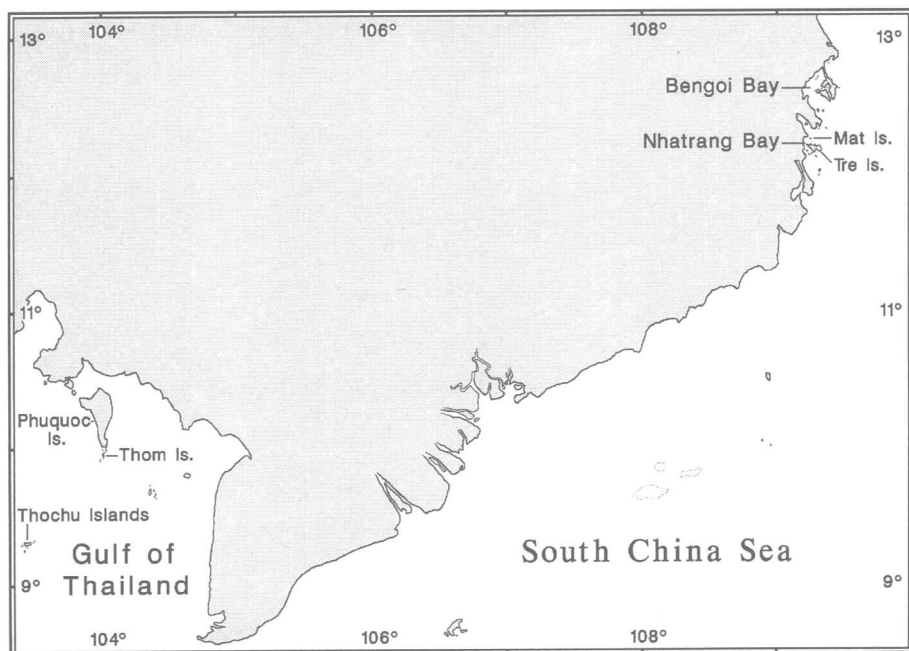


Figure 1. Map showing localities mentioned in the text.

Types and representative specimens are deposited at the Zoological Institute, St. Petersburg (ZISP), the Institute of Marine Biology, Vladivostok (IMBV), the Zoological Reference Collection of Singapore State University, Singapore (ZRC), and at the United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Type material of *Polydorella smurovi* Tzetlin et Britayev, 1985 (ZISP 1/47660 and 2/47661) was also examined.

SYSTEMATIC ACCOUNT

Genus *Polydorella* Augener, 1914, emended

Type Species.—*Polydorella prolifera* Augener, 1914, by monotypy.

Diagnosis.—Body short with constant number of segments, 15 or 16. Prostomium entire or incised on anterior margin, caruncle short or absent. Segment 1 reduced, without notopodia or notosetae; neuropodia with or without neurosetae. Segment 5 slightly modified, with two types of modified spines, arranged in short, slightly curved or straight rows; one type of spine with enlarged distal end and another simple, acicular; capillary notosetae present or absent; capillary neurosetae present, similar in number and shape to neurosetae of segments 4 and 6. Neuropodial hooded hooks from setiger 8, slightly curved, bidentate, with secondary tooth closely applied to main fang, with constriction on shaft; accompanying capillaries absent. Branchiae few, one or two pairs from segment 7, or entirely absent. Pygidium reduced. Habitat: forms mud tubes on sponge surfaces. Asexual reproduction by paratomy.

Remarks.—Neuropodial capillaries accompanying hooded hooks were reported in *P. smurovi* by Tzetlin and Britayev (1985) but were not found by the author in type material of the species.

KEY TO SPECIES OF *POLYDORELLA*

- 1a. Branchiae absent *P. smurovi* Tzetlin et Britayev
 1b. Branchiae present 2
 2a. Two pairs of branchiae *P. stolonifera* (Blake et Kudenov)
 2b. One pair of branchiae 3
 3a. Major spines of segment 5 with apical cavity and bristle-topped projection
 *P. prolifera* Augener
 3b. Major spines of segment 5 without apical cavity and bristle-topped projection
 *P. dawydoffi* new species

Polydorella dawydoffi new species

Figures 2, 3

? *Polydorella prolifera*.—Fauvel, 1930: 36, fig. 8; 1953: 322–323, fig. 169 a–g. [Not *Polydorella prolifera* Augener, 1914].

? Post-larval Chaetopterid.—Gravely, 1927: 78, pl. IX, figs. 12–14.

Type Material.—SOUTH CHINA SEA:—SOUTH-EASTERN COAST OF VIETNAM: Tre Is. of Nhatrang Bay, 12°10'19"N, 109°16'35"E, from surface of *Haliclona* sp., 8 m, 27 Sep 1988, holotype (ZISP 1/50386), 53 paratypes (2/50387), 10 paratypes (ZRC.1989.2–11); Nhatrang Bay, 12°11'18"N, 109°14'11"E, 7 m, 21 Sep 1988, 57 paratypes (IMBV 1/12221);—GULF OF THAILAND: Thom Is. of Anthoi Archipelago, 9°57'30"N, 104°00'15"E, from surface of *Xestospongia testudinaria*, 7 m, 2 Feb 1986, 22 paratypes (IMBV 2/12222), 30 paratypes (IMBV 3/12223), 10 paratypes (USNM 148722).

Other Material.—SOUTH CHINA SEA:—SOUTH-EASTERN COAST OF VIETNAM: Bengoi Bay, 12°38'7"N, 109°15'11"E, 7 m, mud tubes on surface of *Callyspongia* sp., 19 Sep 1988 (IMBV 4/12224, 5/12225); Nhatrang Bay, 12°12'03"N, 109°13'34"E, 5 m, mud tubes on surface of *Mycale* sp., 21 Jan 1986 (IMBV 6/12226); Nhatrang Bay, 12°10'50"N, 109°13'35"E, 3 m, mud tubes on surface of *Callyspongia* sp., 10 Mar 1986 (IMBV 7/12227); Nhatrang Bay, 12°12'27"N, 109°14'51"E, 3 m, mud tubes on surface of *Haliclona* sp., 23 Sep 1988 (IMBV 8/12228); same locality and habitat, 5 m, mud tubes on sponge, 23 Sep 1988 (IMBV 9/12229, 10/12230); Tre Is. of Nhatrang Bay, 12°10'19"N, 109°16'35"E, 8 m, mud tubes on sponge, 27 Sep 1988 (IMBV 11/12231, 12/12232); Mat Is. of Nhatrang Bay, 12°17'15"N, 109°14'28"E, 6 m, mud tubes on surface of *Petrosia* sp., 22 Sep 1988 (IMBV 13/12233); Nhatrang Bay, 5–10 m, from surface of *Rhaphidophlus erectus*, *Amphimedon* sp., *Mycale* sp., *Niphates* sp., *Polymastia* sp., and *Suberites* sp., Sep 1988 (not preserved);—GULF OF THAILAND: Phuquoc Is., 10°01'12"N, 104°00'00"E, 10 m, from surface of *Xestospongia testudinaria*, 3 Feb 1986 (not preserved); Thochu Islands, 9°17'N, 103°26'E, 8 m, from surface of sponge, 1 Mar 1986 (not preserved).

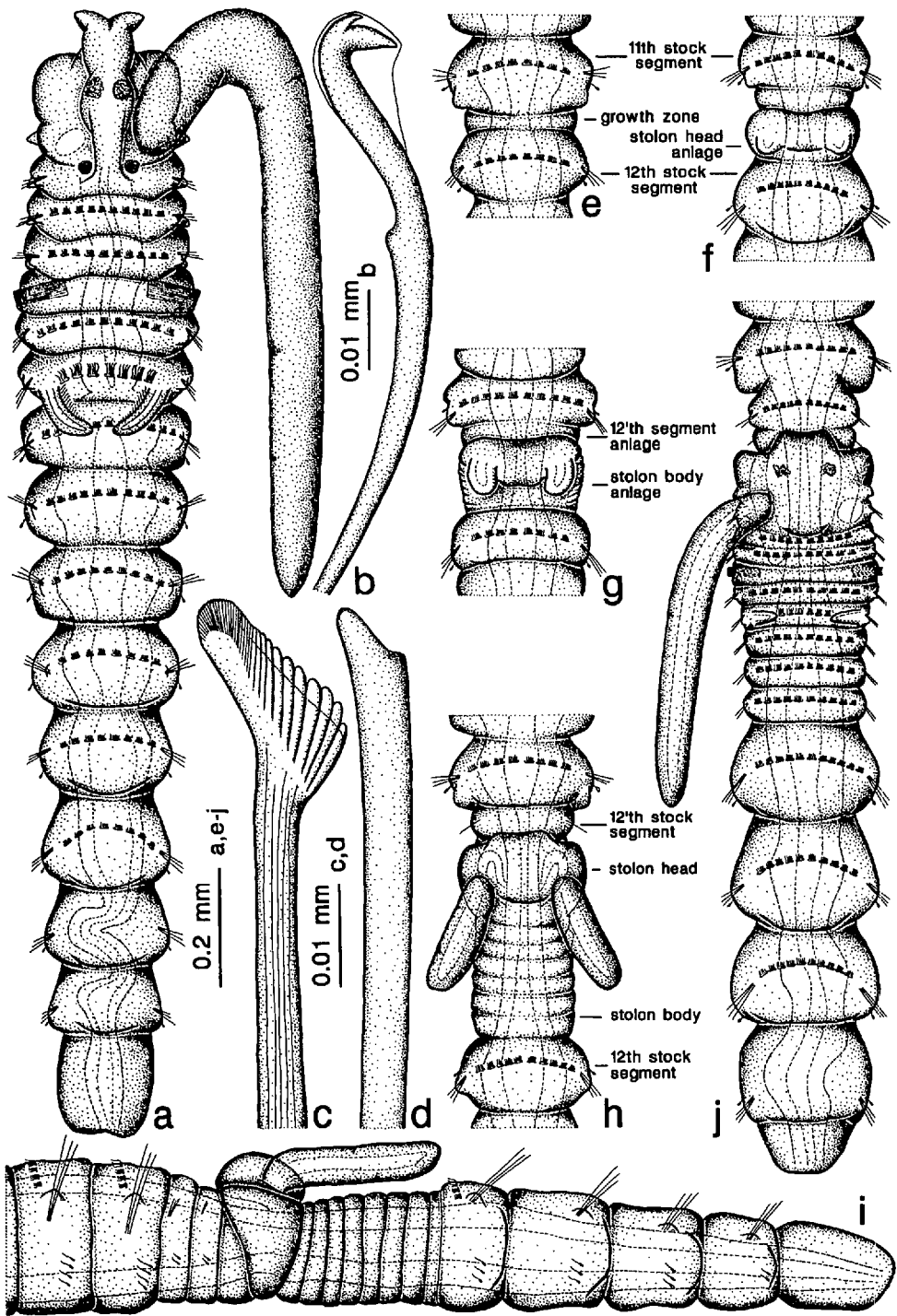
Description of Holotype.—Specimen 2.5 mm long and 0.33 mm wide (at segment 5) for 15 segments. Pigmentation absent. Two white irregularly rounded eye-spots present. Prostomium anteriorly bifid. Caruncle posteriorly extending to middle of segment 2. Nuchal ciliary patches present on either side of caruncle. Nuchal tentacle absent. Palps reaching segment 10–11 (Fig. 2a).

Segment 1 reduced, demarcated from peristomium by indistinct constriction, with neuropodial lobes, without notopodial ones, noto- or neurosetae. Segments 1 to 7 short as if compressed, following ones longer. Podial lobes of segments 2–4, 6 and 7 well developed; smaller on following segments.

Notopodia from segment 2 and neuropodia of segments 2 to 7 with fascicles of unilimbate capillaries. Neuropodia from segment 8 with bidentate hooded hooks only, numbering up to 5 per fascicle; hooks with constricted shafts and

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Figure 2. Morphology and asexual reproduction of *Polydorella dawydoffi* new species. a, holotype, dorsal view; b, neuropodial bidentate hooded hook of segment 8; c, d, heavy modified spines of segment 5; e–j, consecutive stages of paratomic division: e, development of paratomic growth zone between stock segments 11 and 12, dorsal view; f, development of stock segment-forming growth



zone and of stolon head anlage, dorsal view; g, development of stolon body anlage, dorsal view; h, simultaneous differentiation of anterior stolon segments and development of 12' stock segment, dorsal view; i, successive development of posterior stolon segment, lateral view; j, completely developed stolon before separation from stock, dorsal view.

reduced angle between main fang and apical tooth (Fig. 2b). Specialized posterior notosetae absent.

Segment 5 similar in size to segments 4 and 6, without noto- or neuropodial lobes, with dorsal and ventral fascicles of unilimbate capillary setae. Modified spines of two types: first type, up to 9 in number, distally enlarged, with denticulate edge (Fig. 2c); second type, up to 6 in number, simple, acicular with subapical shelf on convex side (Fig. 2d).

Single pair of branchiae on segment 7. Ciliary bands located on segments 3 to 13, excluding segment 5. Longest cilia present on segment 7, extending onto branchiae.

Pygidium elongated with terminal anus.

Narrow pharynx extending posteriorly to setiger 8. Intestine broad, gradually narrowing in posterior segments. Gizzard-like structure in digestive tract absent.

Glandular pouches present from segment 6, well developed to segment 9.

Variability.—Most specimens at different stages of asexual reproduction. Single, non-reproducing specimens rare, 1.5–2 mm in length for 14–15 segments (pygidium excluded). Largest single individual 3 mm long for 17 segments and had two endoparasitic copepods attached. Possibly, the copepods may interfere with the process of paratomy and cause abnormal growth. Two endoparasitic copepods were present in segments 9 and 10 of the holotype. Thus, normal number of segments of the species is probably 15.

In all specimens examined, caruncle extends posteriorly to the beginning or to the middle of segment 2. Branchiae occur only on segment 7. Pigmentation is usually absent, occasional specimens with black pigment grains scattered anteriorly and posteriorly. Two white eye-spots apparent in living specimens but invisible in preserved ones.

Remarks.—*Polydorella dawydoffi* is very similar to *P. prolifera* from West Australia. According to Augener, *P. prolifera* has incised prostomium, branchiae on segment 7 only, dorsal and ventral fascicles of unilimbate capillaries of segment 5, and major spines of segment 5 similar to those of *P. dawydoffi*. Some differences between the two species exist, however, in the process of paratomic division. Two syntypes of *P. prolifera* were redescribed by Blake and Kudenov (1978). Although noting that both specimens were slightly damaged, they were able to provide a more detailed description of the morphology of first type of major spines of setiger 5: “distally enlarged, with one edge fenestrated and surrounding cavity and other bearing elongated bristle-topped projection” (p. 271). Accordingly, the spines of *P. prolifera* differ from those of *P. dawydoffi*.

Polydorella dawydoffi differs from both *P. stolonifera* and *P. smurovi* in the number of branchiae, and in the form of the modified spines of setiger 5. The new species differs from *P. stolonifera* also in the presence of a dorsal fascicle of capillaries on setiger 5.

The presence of two white branched eye-spots on the prostomium is one of the characteristic features of living *P. dawydoffi*.

Asexual Reproduction.—Most of examined the *P. dawydoffi* individuals were reproducing asexually by paratomy. The process begins with the development of a growth zone between segments 11 and 12 (Fig. 2e) of the parental animal or stock. Cell proliferation in this zone leads to the appearance of a head anlage. Shortly after that, the growth of palps on the head anlage commences (Fig. 2f), followed by the development of trunk segments (Fig. 2g). Later, this body anlage, apparently simultaneously, differentiates into a few anterior segments (Fig. 2h);

other segments of the new individual are budded off in succession (Fig. 2i). Although it is difficult to determine the exact number of segments differentiating simultaneously, the best estimate is probably 6 to 8, whereas the number of segments developing in succession is 4 to 2, respectively. During segment formation, outgrowths of the intestine emerge from the palp level toward the anterior end of the stolon head, later forming a stolon pharynx. Thus, the head and the first 10 segments of the new individual or primary stolon are formed in the middle of the parental animal. Stolon segments may be distinguished from parental ones by their smaller size. As the process continues, the stolon head differentiates into a prostomium, having a pair of white eye-spots, and into a peristomium with pharynx and palps. Branchiae and setae develop on the stolon segments (Fig. 2j). Finally, the completely developed 14-segmented stolon (with anterior end composed of head and 10 new segments, and posterior end composed of four parental setigers and pygidium) is separated from the parental individual (paratomic division).

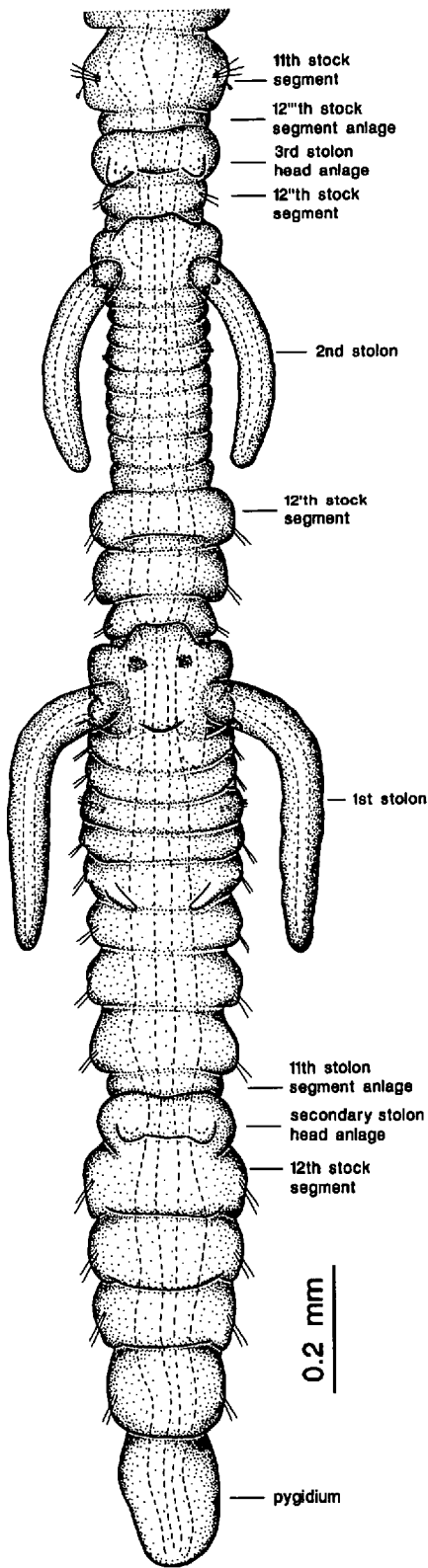
At the beginning of asexual reproduction, the paratomic growth zone splits into two zones. The posterior section is responsible for the stolon formation, whereas the anterior one produces new stock segments (Fig. 2f-j). Thus, the parental individual commences to prepare for its impending loss of segments just after the beginning of asexual reproduction. Stock individuals with segments 12', 13', and 14' (' defines newly developed segments of the stock individual after appearance of the stolon) developing in front of the stolon usually occur (Fig. 2j). An individual having a completely developed segment 14', anlage of segment 15', and a pygidium was found only once. No stock individuals were observed with both segment 15' and pygidium completely developed before the separation from stolon. Probably, stock pygidium normally develops just after paratomic division, and stock segment 15' differentiating later.

The paratomic growth zone of stolons usually starts to develop shortly after or even before the stock separation. The subsequent development of the secondary stolon repeats the described course of events. It is noteworthy that the secondary growth zone develops behind stolon segment 11 soon after its formation or even just after the appearance of an anlage of this segment. So, new growth zones may mistakenly appear to develop after stolon segment 10.

In the parental animal, a new paratomic growth zone usually starts to develop between segments 11 and 12' shortly after the formation of segment 12', leading to the beginning of a second stolon. New daughter individuals are often formed simultaneously in stock and stolon before separation. This leads to the formation of a worm chain consisting of four, five or even six individuals joined together (Fig. 3).

Remarkably, the stolon individual inherits the parental posterior end, i.e., four setigers and pygidium. Those setigers are not distinguished from anterior ones when newly developed. On the contrary, posterior parts inherited by the "granddaughter" from the "grandmother" are strongly distinguished from anterior one. For example, after division of the worm chain presented in Fig. 3, the last individual inherits the posterior end belonging to the primary stock. The segments of this end are distinguished from all others, and consist of large cells up to 25 μ m in diameter, filled with black granules. The fate of the posterior-most end remains unknown.

Asexual reproduction in *P. dawydoffi* was observed in January to March and in September, sexual reproduction was not noted.



Ecology.—*Polydorella dawydoffi* builds small mud tubes on the surface of sponges *Rhaphidophlus erectus* Thiele, *Xestospongia testudinaria* (Lamarck), *Amphimedon* sp., *Callyspongia* sp., *Haliclona* sp., *Mycale* sp., *Niphates* sp., *Petrosia* sp., *Polymastia* sp., and *Suberites* sp. The tubes are usually 1.5–2 mm long and 0.4 mm wide. The species is common in coastal waters at depths between 3 and 10 m. It forms aggregations on the sponges surfaces with a density of up to 130 individuals cm^{-2} . Large aggregations often occurred on one sponge while neighbouring conspecific sponges lacked inhabitants.

Etymology.—The species is named in honour of the Russian-French zoologist Prof. Konstantin N. Dawydoff who devoted much of his life to the exploration of the marine invertebrates of Indo-China.

Distribution.—South China Sea.

DISCUSSION

This study supports Tzetlin and Britayev's reestablishment of the genus. The three earlier described species together with the new one form a distinct group of species related in morphology, ecology and reproduction. As all known *Polydorella* species are associated with sponge surface, a unique feature within the polydorids, it is suggested that the characteristics (apomorphies) of the genus were developed in the most common ancestor in association with this specific habitat. It is noteworthy that polydorid species boring into sponges, *Polydora spongicola* Berkeley et Berkeley, *Polydora colonia* Moore, and *Boccardia* sp. (author's unpubl. data), do not demonstrate neither tiny size nor any kind of asexual reproduction. It should also be noted that asexual reproduction by paratomy in the family Spionidae, except of *Polydorella* species, has been reported only in *Polydora tetrabranchia* Hartman boring into dead shells (Campbell, 1956).

In summary, the genus *Polydorella* includes four species, all described from the Indo-West-Pacific region: *P. prolifera* from the West Australia coast, *P. stolonifera* from the southeastern Australia coast, *P. smurovi* from the Red Sea, and *P. dawydoffi* new species from the South China Sea. The report of *P. prolifera* from the Red Sea by Amoureux et al. (1978) is accompanied by a very short description; the specimens agree with the *Polydorella* diagnosis, but the specific identify requires confirmation. The report of *P. prolifera* from equatorial coast of Somalia from the surface of red algae by Cantone (1987) is not accompanied by any description, but judging from their ecology, the specimens likely belong to another genus. Specimens reported by Gravely (1927) from Indian coastal waters from the surface of a sponge as "postlarval Chaetopterid", and by Fauvel (1930, 1953) as *P. prolifera*, appear to be the same as *P. dawydoffi*. *Polydorella novaegorgiae*, described by Gibbs (1971) from the Solomon Islands, and noted by Shin (1982) from Hong Kong waters, belongs to the genus *Pseudopolydora*.

All described *Polydorella* species are known to include paratomy in their life cycle, have a specific localization of the growth zone and appear to have a specific constant number of segments. In *P. prolifera*, *P. stolonifera*, and *P. smurovi*, the growth zone is reported to develop between segments 10 and 11; in contrast, in *P. dawydoffi*, the growth zone appears between segments 11 and 12. *P. prolifera*

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Figure 3. Paratomic chain of *Polydorella dawydoffi* new species with five developing individuals.

and *P. stolonifera* are reported to have 16 segments (Blake and Kudenov, 1978) while *P. dawydoffi* and *P. smurovi* (author's examination of type material) have 15 segments.

Sexual reproduction has been reported for *P. smurovi* only: the species produces egg cocoons with about 30 embryos (Tzetlin and Britayev, 1985). This kind of reproduction appears to occur in other *Polydorella* species, and the life cycle of species of the genus thus includes an alternation of sexual and asexual reproduction. A pelagic dispersal stage is "needed" in *Polydorella* life history for colonizing new substrata.

The genus *Polydorella* is similar to the monotypic genus *Amphipolydora* Blake, 1983. The latter is of small size (up to 2.3 mm long for 25 segments), has weakly developed setiger 1, two types of spines in setiger 5, no branchiae, reduced pygidium and is capable of asexual reproduction (Blake, 1983). The main differences between the two genera are connected with the kind of asexual reproduction and with their ecology. *Amphipolydora* species reproduces by architomy and inhabits sandy bottoms, while *Polydorella* species reproduce by paratomy and inhabit surface of sponges. They differ also in that *Amphipolydora* has hooded hooks without shaft constrictions, beginning on segment 7, instead of hooks with constrictions, beginning on segment 8. Therefore, the two genera appear to constitute two monophyletic polydorid sister groups that should be further evaluated in future phylogenetic analysis of the family.

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